# WHAT IS THE UNIT OF NATURAL SELECTION?

Mae-Wan Ho
Biology Department
Open University
Milton Keynes, U.K.

Peter T. Saunders
Mathematics Department
Queen Elizabeth College
London, U.K.

Received April 8, 1980; March 9, 1981

ABSTRACT: Contemporary neo-Darwinism requires that the unit of natural selection is the gene, rather than the individual or the species. Yet the 'gene' on which the theory is based has no independent existence, but is a construct within the theory itself.

* * *

Darwinian natural selection is supposed to act on individuals, not on groups or species. Consequently, the major problem in present-day evolutionary studies is to try to explain how characteristics which are seen to benefit groups could have evolved by the natural selection of individuals. The problem becomes most acute in ethology, particularly in the paradox of 'altruism'(Wilson, 1975, p.3):

> "..This brings us to the central theoretical problem of sociobiology: how can altruism, which by definition reduces personal fitness, possibly evolve by natural selection?"

The answer turns out to be the theory of 'kin-selection'(Hamilton, 1964). The altruist, in apparently sacrificing himself, or at least, his reproductive potential, is in fact ensuring the reproduction of copies of his own genes, a definite proportion of which he shares with his relatives. The unit of selection is thus neither the group nor the individual, but the *gene*. This conclusion lends a new significance to the mathematical theories of Fisher (1930) and Haldane(1932): the 'genes' which in those early days had been little more than modelling entities in population genetics, now gains a *literal* interpretation within sociobiological theory.

But this trend towards the emphasis on genes as the units of natural selection had developed, perhaps independently of sociobiology, within the context of neo-Darwinian theory itself. Williams (1966) in an attempt to "purge biology of unnecessary distractions that impede the progress of evolutionary theory" criticised group selection in all its forms. He argues rightly against the tendency of many biologists to see adaptation "in purely fortuitous effects", and to invoke natural selection "to resolve problems that do not exist". His recommendation is to adopt the "doctrine" that adaptation is a "special and onerous concept" which should be used only when it is necessary (Williams, 1966, pp4-5, italics ours):

> "..When it must be recognized, it should be attributed to no higher a level of organization than is demanded by the evidence. In explaining adaptation, *one should assume the adequacy of the simplest form of natural selection, that of alternative alleles in Mendelian population*, unless the evidence clearly shows that this theory does not suffice."

This is a rigorous restatement of the 'bean-bag' genetics approach of Fisher and Haldane which has long been objected to by Mayr (1959). Mayr insists that natural selection acts on whole genotypes, the success of which depend on 'harmonious' combinations of interacting genes. Sewall Wright (1930) has come to a very similar point of view much earlier on (see also recent statements (Wright, 1969; 1978; 1980)).

Williams, however, points out that natural selection cannot act on genotypes for "meiosis and recombination destroy genotypes as surely as death". Thus (Williams, 1966, p.24, italics ours):

> "..It is only the meiotically dissociated fragments of the genotype that are transmitted in sexual reproduction, and these fragments are further fragmented by meiosis in the next generation. If there is an *ultimate indivisible fragment* it is, by definition, 'the gene'..."

This attitude is epitomised in Dawkins' 'selfish gene' concept (Dawkins, 1976, p.12):

* * * * * * *

Evolutionary Theory 5:169-172 (May, 1981)
The editors thank A. Chovnick and W. Wimsatt for help in evaluating this paper.

> "..I shall argue that the fundamental unit of selection, and therefore of self-interest, is not the species, nor the group, nor even, strictly the individual. It is the gene, the unit of heredity.."

But the 'gene', that 'unit of heredity' on which the entire edifice of neo-Darwinism rests, is a splendid example of the 'fallacy of misplaced concreteness', defined by Whitehead(1926) as "the error of mistaking the abstract for the concrete". The gene of evolutionary biology as that inviolate (barring rare mutations) sequence of DNA that codes for a polypeptide is at least twenty years out of date. The same processes of meiosis and recombination that break up genotypes as surely break up genes. Intragenic recombination has been a textbook topic for more than ten years. Benzer's (1957) classic experiments in fine-structure gene mapping showed that the unit of recombination is, in fact, single nucleotide pairs. Thus, there is no "ultimate indivisible fragment" - except the single nucleotide pairs - on which natural selection could be said to act.

Nor can we rely on the concept of gene as a unit-of-function to get us out of this impasse, for we do not know what the unit of function is, if such exists. The history of genetics is littered with attempts at an atomistic formulation of gene function. Their consistent failure is shown by the ubiquitous use of such terms as 'epistasis', 'pleiotropy' and 'multifactorial inheritance'. During the past three or so years, even that familiar entity that codes for a single polypeptide has been shown to be a collection of smaller units separated by non-coding sequences (see Weatherall and Clegg, 1979). The causal connections between the genetic material and proteins show yet further, previously unsuspected complications involving DNA rearrangements, and enzyme systems which process products of transcription into messenger RNA (see recent issue of Science, 19 Sept., 1980, devoted entirely to recombinant DNA).

We agree with Dawkins that so long as one accepts the neo-Darwinian framework, the selfish gene concept is its logical conclusion. We see this, however, not as a triumph of the theory, but rather as its reductio ad absurdum. Neo-Darwinism depends on there being 'genes', atomistically separable entities subject to mutation and recombination. Yet neither in a structural nor in a functional sense do such entities exist. Surely this must be regarded as a fundamental weakness in the theory!

That Dawkins himself is not totally unaware of this difficulty is suggested by his recent attempt to retreat to selfish 'replicators' as the units of natural selection (Dawkins, 1978, p.62):

> "..Selection means differential survival, and the units which survive in the long run are not individuals but replicators (genes or small fragments of genome).."

This attempt fails for the same reasons that the selfish gene thesis is untenable. On account of the processes of mutation and recombination, 'replicators' do not have an identity and hence can never be said to survive, especially in the 'long run'. The frequent error to believe otherwise is simply due to a confusion between the supposed function of the gene, which survives, and the gene itself, which does not. This distinction is all the more important when it is recognized that the same function is often served by entirely different genes or gene combinations.

Considerable unease is presently felt within the neo-Darwinist camp concerning the unit of natural selection precisely because it poses such difficulties for neo-Darwinian theory. On the one hand, Dawkins (1978) criticises almost all of the leading exponents of neo-Darwinism for their failure to purge the last vestige of organisms, or individuals, out of their models of natural selection. On the other hand, Alexander and Borgia (1978), for example, see a need to resolve "the discrepency between the widely accepted unit of selection (the individual) and the obvious units of inheritance (chromosomes and parts of chromosomes)", but are unhappy about the selfish gene concept. They offer their own solution, which is, to re-instate group selection of *genes* at all levels of organization. In particular, they call for the re-consideration of the natural selection of genomes as "coalitions" of genetic units which exert a "power of the collective" against "outlaw genes". But this postulated mystical conflict between genes, like that invoked by Williams (1979) to 'explain' the *absence* of adaptive sex ratio, is contrary (yet again) to an elementary lesson of molecular genetics. Most of the DNA in genomes are redundant 'silent genes' serving no useful function whatsoever. Genic conflicts, if such exist, should lead to the rapid elimination of these free-loaders from the genome.

In fact, since the original version of this paper was submitted, precisely this question has been raised in the concept of 'selfish DNA'(Doolittle and Sapienza,1980; Orgel and Crick, 1980) - the proposal that there are large classes of DNA with no phenotypic expression whose sole 'function' is to survive within genomes. In particular, Doolittle and Sapienza are critical of the majority who are "wedded to the 'phenotype paradigm'"- the notion that the major and perhaps the only way that a gene or any piece of DNA can ensure its own perpetuation is by ensuring the perpetuation of the organism it inhabits. If the 'selfish DNA' concept is right, then the evolution of the phenotype becomes even further decoupled from that of the DNA or genes, and neo-Darwinism's claim to provide a complete explanation of evolution becomes highly questionable, unless by evolution, we mean only the evolution of DNA.

By far, the major and deepest difficulty inherent in a theory of evolution by the natural selection of genes is that it leaves *organisms* out of consideration altogether; that is, it leaves out the very entities that are to be explained. In collapsing the vast complexity of the evolution of organisms into the natural selection of genes, neo-Darwinism has regressed into the total mystification of evolutionary phenomena. In the last analysis, the 'gene' is little more than one of those occult Aristotelean 'qualities' that were supposed to be the causes of phenomena[1].

Elsewhere, we have argued in detail for an alternative approach to the study of evolution, in which we proposed that the intrinsic dynamical structure of the epigenetic system, in its interaction with the environment, is the source of non-random variations which direct evolutionary change (Ho and Saunders, 1979). The real mechanisms of evolution therefore, consist of the epigenetic processes involved in organism-environmental interactions, and in the canalisation and genetic assimilation of novel developmental responses arising out of those interactions (Ho and Saunders, 1981). This by no means exhaust the alternatives to neo-Darwinism (Saunders and Ho, 1981). In a more recent paper (Ho and Saunders 1981a) we have attempted to outline a newer and infinitely richer framework for evolutionary research.

## REFERENCES

Alexander, R.D. and Borgia, G. (1978). Group selection, altruism, and the levels of organization of life. *Ann. Rev. Ecol. Syst.* 9: 449-474.
Benzer, S. (1957). The elementary units of heredity. In *The Chemical Basis of Heredity* (W.D. McElroy and B. Glare, eds.) pp.70-93, John Hopkins Press, Baltimore.
Dawkins, R. (1976). *The Selfish Gene*. Oxford University Press, Oxford.
Dawkins, R. (1978). Replicator selection and the extended phenotype. *Zeit. Tierpsychol.* 47: 61-76.
Doolittle, W.F. and Sapienza, C. (1980). Selfish genes, the phenotype paradigm and

* * *

[1] We are grateful to Professor Wolfe Mays for this remark.

genome evolution. *Nature* 284: 601-603.

Fisher, R.A. (1930). *The Genetical Theory of Natural Selection.* Clarendon Press, Oxford.

Haldane, J.B.S. (1932). *The Causes of Evolution.* Longmans, London.

Hamilton, W.D. (1964). The genetical theory of social behaviour I and II. *J. Theor. Biol.* 7: 1-16; 17-32.

Ho, M.W. and Saunders, P.T. (1979). Beyond neo-Darwinism: an epigenetic approach to evolution. *J. Theor. Biol.* 78: 573-591.

Ho, M.W. and Saunders, P.T. (1981). Adaptation and natural selection: mechanism and teleology. In *Against Reductionism: Towards a Liberatory Biology* (M. Barker, *et al*, eds.). Allison and Busby, London.

Ho, M.W. and Saunders, P.T. (1981a). 'Necessity the mother of invention' - towards a new evolutionary paradigm. (submitted for publication).

Mayr, E. (1959). Where are we? *Co. Spr. Harb. Symp. Quant. Biol.* 24: 1-14.

Orgel, L.E. and Crick, F.H.C. (1980). Selfish DNA: the ultimate parasite. *Nature* 284: 604-607.

Saunders, P.T. and Ho, M.W. (1981). On the increase in complexity in evolution II. The relativity of complexity and the principle of the minimum increase. *J. Theor. Biol.* (in press).

Weatherall, D.J. and Clegg, J.B. (1979). Recent developments in the molecular genetics of human hemoglobin. *Cell* 16: 467-479.

Whitehead, A.N. (1926). *Science and the Modern World.* Cambridge University Press, Cambridge.

Williams, G.C. (1966). *Adaptation and Natural Selection.* Princeton University Press, Princeton.

Williams, G.C. (1979). The question of adaptive sex ratio in outcrossed vertebrates. *Proc. R. Soc. Lond.* B 205: 567-580.

Wilson, E.O. (1975). *Sociobiology.* Belknap Press, Cambridge, Mass.

Wright, S. (1930). The genetical theory of natural selection. A review. *J. Heredity* 21: 349-356.

Wright, S. (1969; 1978). *Evolution and the Genetics of Populations*, vols. II and IV. University of Chicago Press, Chicago.

Wright, S. (1980). Genic and organismic selection. *Evol.* 34: 825-843.